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Timing of reproduction and fledging success in the coot *Fulica atra*: evidence for a causal relationship

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Summary

1. We investigated the relationship between hatching date and fledging success in the European coot (*Fulica atra*).

2. The production of fledglings per brood increased in the first half of the season and decreased in the second half, independent of clutch size or egg size. We tested experimentally whether this convex seasonal pattern is causally related to date.

3. The timing of parental care was manipulated by exchanging complete first clutches that differed in stage of incubation. Our experiments tested whether the natural variation in fledging success was due to (i) factors related to date (date hypothesis), (ii) factors related to parental and/or territory quality (parental quality hypothesis), or to a combination of both factors.

4. In the first half of the season, an experimental advance of the timing of parental care reduced fledging success, while an experimental delay raised it. In the second half of the season the opposite was found. Fledgling production by experimental pairs did not differ systematically from that of control pairs raising young at the same time.

5. Thus, the results were consistent only with the date hypothesis, and we conclude that timing of breeding and fledging success are causally related in the coot.

6. Independent of date, age of male parents was positively correlated with fledging success, suggesting that aspects of parental quality play an additional role.

Key-words: European coot, laying date, nestling survival, parental quality, reproductive success.

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Introduction

The production of offspring in birds usually depends strongly on both clutch size and laying date (e.g. Cavé 1968; Perrins & McCleery 1989; Daan, Dijkstra & Tinbergen 1990; Tinbergen & Daan 1990). The variation observed in these traits could be the outcome of individual optimization when individual pairs adjust their decisions concerning both traits to their individual circumstances (Drent & Daan 1980; Högstedt 1980). This implies that fitness consequences of variation in a trait must be quantified experimentally, because consequences of alternative decisions cannot be predicted from natural variation. So far, most studies have concentrated on explaining the variation in clutch size (review in Dijkstra *et al.* 1990). Evidence for individual optimization of clutch size based on measured consequences for both parents and offspring comes from three studies (Pettifor, Perrins & McCleery 1988; Daan *et al.* 1990; Tinbergen & Daan 1990). Experimental studies designed to measure fitness consequences of laying date are few (Parsons 1975; Hunt & Hunt 1976; Nilsson 1990; Hatchwell 1991; Verhulst & Tinbergen 1991). Our aim in this paper is to investigate the relationship between date and an important fitness component, namely fledging success. Our experiments were designed to establish if laying date is causally involved in the seasonal variation in this component of fitness in a population of the coot *Fulica atra*.

There is a seasonal decline in fledging success in most single brooded species (e.g. Perrins 1965; Harris 1967; Murton & Westwood 1977; Newton & Marquiss 1984), whereas in multiple breeders the seasonal variation is less pronounced (review by Daan *et al.* 1989). We chose the coot for timing experiments because they show a distinct convex

seasonal pattern for fledging success of first clutches. We manipulated the timing of parental care, by exchanging clutches of equal size, that differed in laying date (Hunt & Hunt 1976), thereby creating advanced and delayed pairs over most of the season.

We consider two major hypotheses to explain seasonal variation in fledging success. The variation may be due to seasonal variation in the environment affecting all individuals equally (date hypothesis). Alternatively, it may be due to differences among parents and the territories that they occupy (parental quality hypothesis). The two hypotheses are not mutually exclusive. However, they do lead to different predictions for experimental manipulations of date.

The date hypothesis predicts that the experimentally advanced and delayed pairs will follow the natural seasonal trend. Due to the convex seasonal pattern in success, opposite effects of the same time shift are expected in the first and the second half of the season (Fig. 1a). The parental quality hypothesis predicts that fledging success of advanced and delayed pairs will be related to their original hatching date, not to the actual one. Under this hypothesis, the general relationship between date and offspring number will be shifted backward or forward for the advanced and delayed pairs, respectively. When comparing success of experimental pairs to control pairs with the same actual date, opposite effects of the same manipulation are expected in the first and second half of the season (Fig. 1b). For both hypotheses, the convex seasonal pattern leads to the prediction that the same manipulation will have different effects depending on the season. This allows us to separate the effects of the manipulation *per se* from the responses to altered timing.

A mixture of both hypotheses may be formulated as a third hypothesis. Birds may attune their timing of breeding to the situation within their own territory. This could be important if there is a seasonal peak in food abundance of which the timing varies between territories. In this case, both an advance and a delay of the period of parental care would result in a decrease in fledging success (individual optimal date hypothesis, Fig. 1c).

Timing of breeding cannot be manipulated without altering other aspects of the bird or its environment. In our experiment the manipulation of hatching date was confounded with an effect on the length of the incubation period. We assumed that this did not affect our results and the extent to which this assumption could be justified will be evaluated in the discussion. Furthermore, we manipulated the timing of parental care, but not the hatching date of the fostered clutch. This means that our experimental approach is appropriate only when seasonal variation in egg quality is not responsible for the seasonal variation in fledgling success. We will show that differences in egg quality were not involved in the seasonal variation in fledging survival.

Methods

STUDY AREA AND STUDY SPECIES

The data were collected in 1988, 1989 and 1991 in a study area on the edge of the lake Westeinderplassen, 17 km south-west of Amsterdam. The area covers approximately 155 ha and consists of a large number of small artificial islands, used mainly for horticulture and recreation. A more detailed description is given in Cavé & Visser (1985). The number of breeding pairs of the European coot in the study population varied between 135, 157 and 148 in 1988, 1989 and 1991, respectively. The majority of the adult birds in the study area were marked by steel leg rings and numbered neck collars.

Coots are highly territorial during the breeding season (Kornowski 1957; Horsfall 1984c). Both male and female defend territory boundaries, which

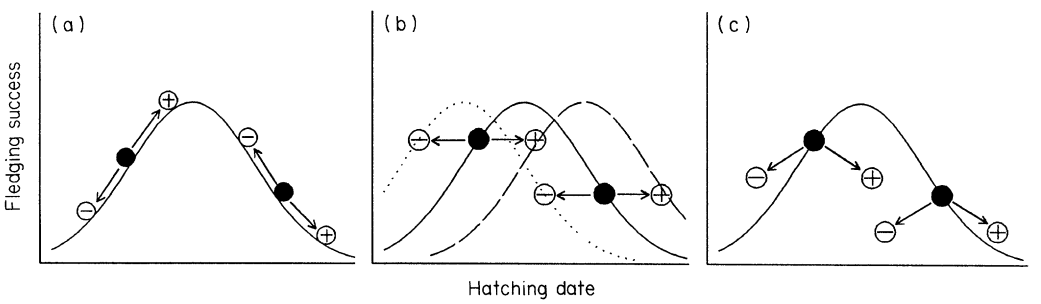

Fig. 1. Expected results under different hypotheses. The control pairs (•) give the natural seasonal trend in fledging success (solid line). Fledging success was defined as the number of young surviving 7 weeks. If date or some factor(s) associated with date are responsible for the trend (date hypothesis) the success of both advanced pairs (−) and delayed pairs (+) will depend on the actual hatching date, and not on the original one. The experimental pairs follow the trend (Fig. 1a). If factors associated with the quality of the parents or their territory are responsible (parental quality hypothesis) the success of advanced (dotted line) or delayed pairs (broken line) will not be affected by the manipulation of the timing of parental care, and the curves will be shifted in time (Fig. 1b). If pairs tune their timing to the specific situation to maximize fledging production (individual optimal date hypothesis), both advance and delay should lead to a reduction of fledging success at any date (Fig. 1c).

often involves fierce fighting (Cramp & Simmons 1980). The coot is a facultatively double-brooded species, in which only the earliest pairs may produce a second brood. Chicks are almost entirely dependent on their parents in the first two weeks following hatching (Horsfall 1984a), and care is biparental. The young are largely self-supporting at an age of 7–9 weeks (Kornowski 1957; Horsfall 1984a).

DETERMINATION OF BASIC BREEDING PARAMETERS

From early March until late June the whole area was checked at least once a week to locate the nest sites. When eggs were found they were marked with permanent ink. Laying date (date of first egg) and clutch size were determined, and parents identified. Laying date was calculated, assuming a laying frequency of one egg per day. The clutch was considered complete when on three consecutive days no additional egg was laid. Incubation occurs from the middle of the laying period onwards, which leads to asynchronous hatching (Horsfall 1984b). In an independent data set the hatching date (HD; 50% of the clutch hatched) is related to CS and LD according to the formula $HD = 0{\cdot}46 * CS + 0{\cdot}95 * LD + 28{\cdot}75$ (obtained by multiple regression, $r^2 = 0{\cdot}99$, $n = 130$; 1st of January is day 1). The length of the incubation period decreased with laying date (slope = −0·05 days/day). This formula was used to obtain the expected hatching dates. The maximum deviation from the actual hatching date found was 2 days.

In 1991, maximum egg length and width (±0·1 mm) were determined using dial callipers. Freshly laid eggs (within one day) were weighed (±0·1 g). Fresh egg mass was estimated as well from size using Hoyt's (1979) equation: $\text{mass} = Kw * \text{length} * \text{breadth}^2$. The calculated mass coefficient Kw for European coots was 0·527 (multiple regression, $n = 90$, $r^2 = 0{\cdot}90$). As eggs were not usually found within one day of laying the estimated mass was used in the analysis.

EXPERIMENTAL PROCEDURE

Timing of parental care was manipulated by exchanging complete first clutches that differed by 10 days in expected hatching date (allowing for one day difference). The exchanged clutches were of equal size (allowing for one egg difference). For one pair the timing of parental care was advanced 10 days by exchanging their clutch, 15 days before the expected day of hatching, with a second pairs' clutch that was expected to hatch in 5 days. The second pair received the clutch of the first pair and, thus, hatching of eggs in their nest was delayed by 10 days. We selected control pairs with clutch sizes and expected hatching dates that matched either an advanced or a delayed pair. Control pairs received the same treatment as experimental pairs, but the expected hatching date of the clutch the pair received was identical to the original expected hatching date. In 1988 this was achieved by exchanging clutches between control pairs which had the same clutch size and expected hatching date. In 1989 and 1991 the clutches were not exchanged, but removed and returned to their original parents. Following this procedure, a total of 52 pairs were advanced and 52 pairs were delayed, while 73 pairs served as controls.

Clutches were transported by boat using a thermos box in which the temperature was kept between 35 and 39 °C. Transport time between nests was 10–20 min and special care was taken to transport control clutches over a similar period. To prevent nest desertion, an equal-sized clutch of warm, hard-boiled eggs was used as a temporary substitute. Most pairs resumed incubation within 10 min after the exchange.

In 1988 first clutches hatching early (HD < 110) or late (HD > 140) in the season were not used for experimental purposes. Individuals that had been advanced, delayed or used for other experiments were not selected for the experiment in the following year.

DETERMINATION OF HATCHING SUCCESS, NUMBER AND MASS OF YOUNG

All nests were checked around the expected day of hatching. Four clutches failed to hatch (two in 1988, one in 1989, one in 1991), although incubation was continued for 1–2 weeks after the expected hatching date. Of these, two pairs were advanced, one was delayed and one was a control. For one control pair it could not be established whether or not eggs hatched. All five pairs were excluded from the analysis because the goal of the experiment was to manipulate the hatching date. The results are based on the remaining 71 controls, 51 delayed and 50 advanced pairs.

The extent of egg loss was determined 2 days before the hatching date of the clutch. In 1991, most nests were checked again 2 days after the mean day of hatching to determine hatching success. The number of surviving young of individual pairs was counted weekly up to 7 weeks of age. The number of young raised was defined as the number surviving 7 weeks. It was not possible to determine the number of surviving young of individual pairs accurately after they reached 7 weeks. Young were caught, weighed and ringed between 3 and 6 weeks of age. The young were ringed with numbered steel leg rings and coloured plastic leg rings.

EXPECTED RESULTS FOR EXPERIMENTAL PAIRS

For the control pairs, the expected number of young

raised (n) can be expressed in terms of original hatching date (OD) and its square (OD^2) (Fig. 4):

$$\ln(n) = a + bOD - cOD^2 \qquad \text{eqn 1}$$

We assumed that n follows a Poisson distribution. Describing the expected number of young for the experimental pairs, both the date and the parental quality hypothesis give explicit predictions for the relation between expected number of young of experimental pairs and the predictor variables. According to the date hypothesis the number of young raised by the experimental pairs should depend on the actual hatching date of the fostered clutch, and not on the hatching date of their original clutch (Fig. 1a). The actual hatching date $AD = OD + MD$ (MD = number of days manipulated; for controls $MD = 0$, advanced $MD = -10$, delayed $MD = 10$). Therefore, the expected relationship between hatching date and the number of young raised is given by:

$$\ln(n) = a + b(OD + MD) - c(OD + MD)^2 \qquad \text{eqn 2}$$

and this can be written as:

$$\ln(n) = a + bOD - cOD^2 + (bMD - cMD^2 - 2cOD * MD) \qquad \text{eqn 3}$$

The part of equation 3 in parentheses describes the expected effect of the manipulation. Note that the constants (a, b and c) have the same values in equations 1, 2 and 3.

Under the parental quality hypothesis, no effect of manipulation is expected. The terms involving MD in equation 3 will not be significant, reducing equation 3 to equation 1. This implies that the number of young raised is determined by the original hatching date.

If both date and parental quality are involved in determining fledging success, success of experimental pairs cannot be described using the original date or the actual date alone. In this case, the manipulation will cause a difference relative to both the success expected at the OD and at the AD. Under the individual optimal date hypothesis, fledging success for both advanced and delayed pairs should be smaller on the actual date than on the original date.

DATA ANALYSIS

The analysis was carried out using the Statistix statistical package (version 3.1, Analytical Software, 1989) and GLIM (NAG, release 3.77). Multiple regression was used for the analysis of clutch size and egg size, Poisson regression for the number of young raised and logistic regression for survival rates. A stepwise backward procedure was followed in the regression analyses. The significance of predictor variables was tested using the change in deviance and degrees of freedom when the variable is dropped from the model.

Dates are presented in Julian date (1 January is day 1; 1 May is day 121).

Results

NATURAL SEASONAL TREND IN CLUTCH SIZE AND EGG MASS

The variation in clutch size with year and hatching date was analysed using multiple regression. Year (tested as group) and date squared significantly decreased the deviance (Table 1). The interaction of year with date and date squared was not significant ($F_{(4,163)} = 0{\cdot}37$; $P = 0{\cdot}82$). With reference to the experiment the hatching date of the clutch and not laying date, is given. Overall, clutch size showed an accelerating seasonal decline in each year (Fig. 2). The elevation differed among years, as indicated by the significance of the factor year, but the slopes did not.

Data on the average egg mass within the clutch are available for 1991. Egg mass decreased signifi-

Table 1. Multiple regression analysis of clutch size (A) and egg size (B). The null model is the model with only the constant fitted. The final model gives all variables that were retained in the model. Significance was tested by dropping parameters one at a time from the full model

		(Increase in)			Estimates of coefficients		
	Parameter	deviance	df	P	1988	1989	1991
A	Null model	272·4	171				
	Final model	223·9	167				
	Constant		1				
	Year	12·8	2	0·01	−2·56	−3·31	−3·10
	Actual date (AD)	3·1	1	0·13	0·19	0·19	0·19
	AD square	5·7	1	0·04	−0·00082	−0·00082	−0·00082
B	Null model	716·3	75				
	Final model	651·6	74				
	Constant						49·35
	Actual date	64·7	1	0·01			−0·073

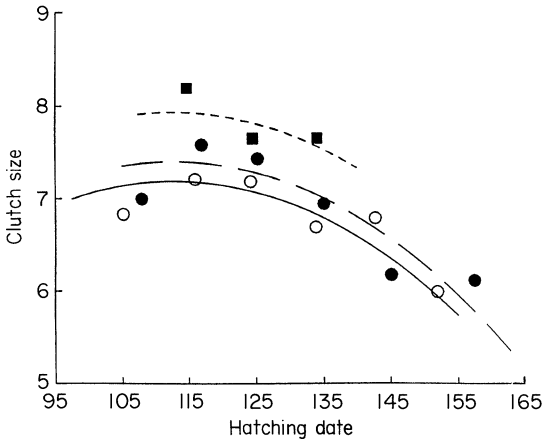

Fig. 2. Seasonal variation in clutch size (control, delayed and advanced pairs combined) averaged over 10-day hatching periods, for 1988 (■), 1989 (○) and 1991 (●).

cantly as the season progressed (Table 1). The calculated average egg mass in the earliest clutches was approximately 2·3 g per egg larger than in the latest (Fig. 3).

To test whether the sampling procedure followed resulted in systematic differences between controls and experimental pairs in the seasonal variation in clutch size or egg size, we added manipulation as group (control, advanced, delayed). In the analysis of clutch size, manipulation (group) and its interactions with date, date squared and year were not significant [$F_{(10,157)} = 0{\cdot}51$; $P = 0{\cdot}88$]. Manipulation (group) and the interactions of manipulation with date were also not significant in the analysis of egg size [$F_{(4,70)} = 0{\cdot}86$; $P = 0{\cdot}49$]. Therefore, we conclude that the seasonal variation in clutch size and egg size for manipulated pairs was similar to control pairs.

HATCHING SUCCESS

Egg survival rate until hatching was 0·98, 0·98 and 0·97 in 1988, 1989 and 1991, respectively, and independent of year (factor), clutch size, egg size (1991), date and manipulation. Hatching success, scored in 1991 only, was 0·91, 0·95 and 0·92 for control, advanced and delayed pairs, respectively, and also independent of clutch size, egg size, date and manipulation (logistic regression; $n = 65$). This implies that neither egg survival nor hatching success were affected by the manipulation of the timing of parental care.

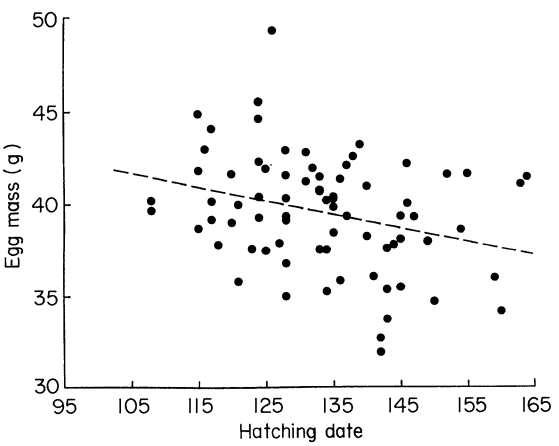

Fig. 3. Seasonal variation in average egg mass in the clutch (control, delayed and advanced pairs combined) in 1991.

NATURAL SEASONAL VARIATION IN FLEDGING SUCCESS

The natural seasonal variation in the number of young raised (n) was analysed using Poisson regression. For control pairs only, year (group), hatching date, date squared, clutch size, and the interaction between year and hatching date contributed significantly to the explained variation (Table 2A). Interactions of clutch size with year, date and date squared were not significant. Furthermore, the average egg size in the clutch and its interactions with clutch size, date and date squared were not significantly involved in 1991. This means that independent of the effects of year and date, the number of first brood young surviving was positively related to clutch size, while there is no detectable effect of egg size.

The results for the variables date and date squared indicate that in all years the success of first clutches can be described by a convex seasonal pattern (see equation 1, Methods). Although clutch size itself showed a seasonal decline (Table 1, Fig. 2), the seasonal variation in fledging success was independent of clutch size (Table 2, Fig. 4). The slope of the ascending as well as the descending part of the curve were significant in 1989 and 1991. In 1988 only seasonal decline in success was present within the control pairs. This was probably due to the fact that the earliest clutches (hatching date <110) were not used for experimental purposes. The slopes of the ascending (1989, 1991 only) and the descending part (all three years) were not significantly different between years. This implies that the main difference between years lies in timing and level of the maximum values within the breeding season.

ARTIFICIAL VARIATION IN FLEDGING SUCCESS

The final model for the control pairs (Table 2A) was taken as the starting point for the analysis of the artificial variation in n. The number of days that the timing of parental care was manipulated (MD) was −9·9 (SD = 1·0) for advanced pairs and +9·9 (SD = 1·0) for delayed pairs. For control pairs $MD = 0$. A graphical presentation of the result of the experiment is given in Fig. 5a and b for the advanced and delayed pairs, respectively. The

Table 2. Poisson regression analysis of the number of young surviving the first 7 weeks after hatching. Regression A is based on the control pairs; regression B and C are based on both control and experimental pairs. For further explanation see Table 1 and text

	Parameter	(Increase in) deviance	df	*P*	Estimates of coefficients 1988	1989	1991
A	Null model	95·7	69				
	Final model	52·5	62				
	Constant		1				
	Year	11·5	2	<0·01	−37·83	−44·74	−51·12
	Original date (*OD*)		1				
	Year × *OD*	10·3	2	0·01	0·64	0·69	0·74
	OD square	12·2	1	<0·01	−0·0027	−0·0027	−0·0027
	Clutch size	8·0	1	<0·01	0·21	0·21	0·21
B	Null model	214·5	168				
	Final model	141·9	156				
	Constant		1				
	Year	7·8	2	0·02	−32·25	−34·91	−39·12
	Original date (*OD*)		1				
	Year × *OD*	5·8	2	0·05	0·55	0·57	0·60
	OD square	20·0	1	<0·01	−0·0023	−0·0023	−0·0023
	Clutch size	3·0	1	0·08	0·089	0·089	0·089
	Manipulation (*MD*)		1				
	Year × *MD*	7·8	2	0·02	0·64	0·67	0·71
	OD × *MD*	21·4	1	<0·01	−0·0053	−0·0053	−0·0053
	MD square	6·5	1	0·01	−0·0034	−0·0034	−0·0034
C	Null model	214·5	168				
	Final model	145·6	161				
	Constant		1				
	Year	11·3	2	<0·01	−34·61	−37·37	−42·26
	Actual date (*AD*)		1				
	Year × *AD*	8·5	2	0·01	0·58	0·60	0·64
	AD square	25·5	1	<0·01	−0·0024	−0·0024	−0·0024
	Clutch size	3·5	1	0·06	0·094	0·094	0·094

relevance of the model describing the artificial variation in statistical terms becomes clear when the variables found are compared with the variables expected under the date hypothesis (equation 3, Methods). The variables above the dashed line (Table 2B) describe the annual seasonal trend given by the control pairs (compare with Table 2A). The remaining variables describe the effect of the manipulation (Table 2B, below the dashed line). These are the variables expected under the date hypothesis (Methods, part of equation 3 between parenthesis). Because of the interaction between year and original date (*OD*) in the controls (Table 2A), the interaction between year and *MD* (*YR***MD*) is found (following $YR(OD + MD) = YR{*}OD + YR{*}MD$). The total contribution of manipulation on the original hatching date, as given by the difference between the minimal model and the final model is significant (delta deviance = 23·0, delta df = 5, $P < 0{\cdot}001$). Further note that within years the regression coefficients for *OD* and *MD* (Methods, coefficient *b* in equation 3), for *OD* squared and *MD* squared (coefficient *c* in equation 3) and for *OD***MD* (2*c*) are close to the expected values. This indicates that experimental pairs follow the natural seasonal trend of the year involved.

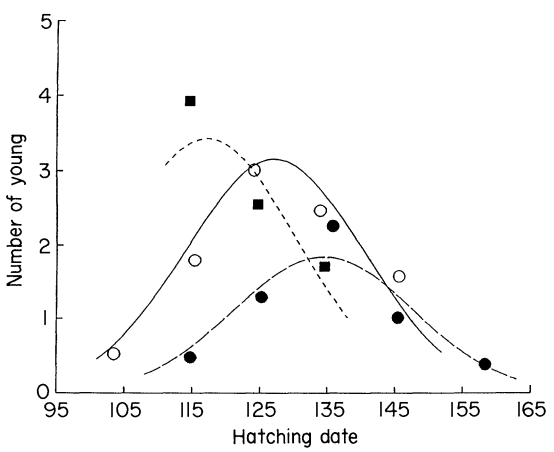

Fig. 4. Seasonal variation in the number of 7 weeks young of control pairs averaged over 10-day hatching periods, for 1988 (■), 1989 (○) and 1991 (●).

Clutch size did not contribute significantly to the explained variance in *n* ($P = 0{\cdot}08$) when analysing the experimental groups together, the interaction between clutch size and *MD* was not significant ($P = 0{\cdot}16$). This means that the relationship between

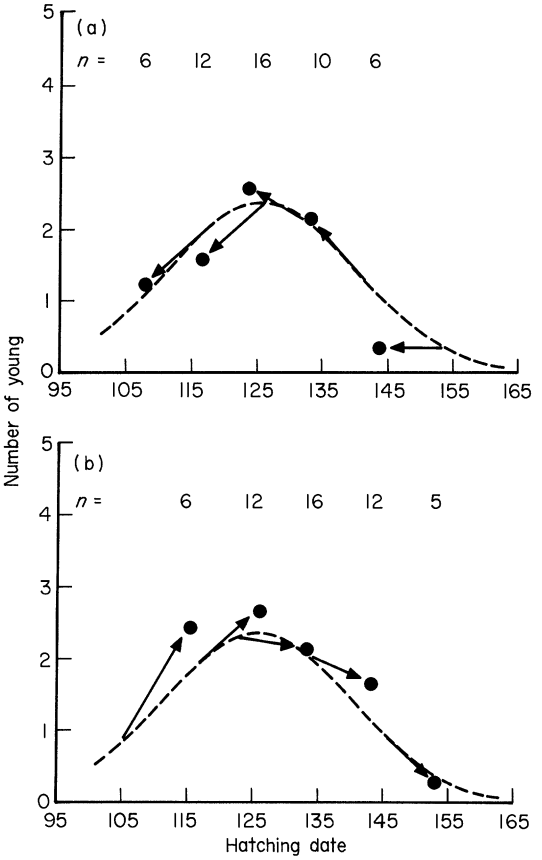

Fig. 5. The number of 7 weeks young in relation to hatching date for (a) advanced pairs and (b) delayed pairs. The curve gives the average seasonal trend in success of control pairs. Dots (•) represent average values over 10-day hatching periods for experimental pairs. Both the line and the average values were corrected for non-date effects, year and clutch size (Table 2c). The arrows give the direction and the effect of the manipulation. The tail of the arrow gives the expectation for parents at the original hatching date. The head of the arrow gives the actual number found.

clutch size and fledging success for experimental pairs did not differ significantly from the controls. In 1991, the actual average egg size, the difference between the actual and the original egg size (for experimentally advanced or delayed pairs), and interactions between the actual egg and clutch sizes, date, date squared and manipulation were not significantly involved in the success of the first clutch. We therefore conclude that egg size did not influence the variation in fledging success.

When analysing the number of young raised in relation to the actual hatching date, no significant additional effect of manipulation was found (Table 2C). This again pleads against both the parental quality hypothesis and the individual optimal date hypothesis. The minimal model considered equals the final model. This means that after manipulation, the actual hatching date determines the number of young raised. The difference between the final models, taking the original date and the effects of manipulation (Table 2B) or taking the actual date (Table 2C), was not significant (delta deviance = 3·7, delta df = 5, $P = 0{\cdot}59$). Clutch size was near significance ($P = 0{\cdot}06$), indicating that independent of the effects of year (group) and hatching date pairs with large clutches tend to raise more young than pairs with small ones.

The date hypothesis and the parental quality hypothesis are not mutually exclusive. We therefore tested whether, in addition to the effects of date, an effect of quality was detectable. Manipulation as a group variable (control, advanced, delayed) and its interactions with the other variables were added to the model based on the actual date (Table 2C). None of the variables added showed significance (delta deviance = 11·0, delta df = 10, $P = 0{\cdot}36$). Thus, the actual hatching date determines the number of young surviving, because the manipulated pairs follow the general seasonal trend. Advancing a pair results, early in the season, in a smaller number of young than expected on the original hatching date; late in the season, however, a larger number is found (Fig. 5a; arrows and dots). Delaying gives the opposite result (Fig. 5b; arrows and dots).

SURVIVAL PATTERN AFTER HATCHING; WHERE DOES THE DATE EFFECT ARISE?

Having established that a pairs' fledging success is determined by the hatching date of the young, we tried to assess in which phase of the parental care period differences in chick survival in relation to date arise. This could be a significant step in the search for the factor(s) responsible for the date effect. The survival of young in the first 7 weeks after hatching for control and manipulated pairs together is given in Fig. 6. A logarithmic scale is used to visualize weekly survival rates. Survival rates were analysed using logistic regression. Com-

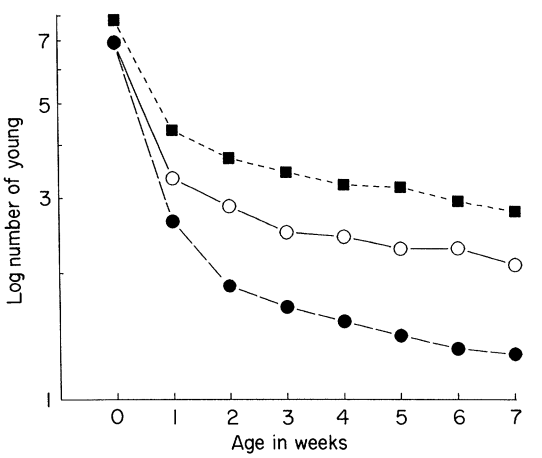

Fig. 6. Number of surviving young (logarithmic scale) in relation to age (control, delayed and advanced pairs combined) for 1988 (■), 1989 (○) and 1991 (•).

paring years, the overall survival rate between hatching (week 0) and week 7 in 1988 and 1989 (0·36 and 0·30, respectively) was significantly higher than in 1991 (0·18; delta deviance = 31·6, delta df = 1, $P < 0{\cdot}001$), but not significantly different between 1988 and 1989. Within years, weekly survival rates were lowest in the first (average rate 0·47) and, especially in 1991, in the second week after hatching (average rate 0·80). Weekly survival rates from week 2 to week 7 were relatively constant within years, the average weekly rate was 0·94 (SD = 0·02) and not significantly different between years.

In the analysis of the seasonal variation in weekly survival rates, only in the first and the second week a convex pattern was found. Taking the two weeks together, a model was constructed in which year (group), the actual hatching date, the actual date squared and the interactions between year and the actual hatching date contributed significantly to the explained variation (Table 3). No additional effect of manipulation (as a group) could be detected over this period. As the residual variation is larger than expected (scale parameter = 1·55) the use of *F*-tests might be considered. In that case, the contribution of all variables, except the interaction between year and actual date ($P = 0{\cdot}09$), remain significant. Given the seasonal trend, the survival levels over the first 2 weeks were significantly lower in 1991 than in 1988 or 1989. Within each year, the highest survivals were found in mid-season (Fig. 7a). Eggs of earlier and later pairs suffer higher mortality rates, and this was causally related to date. The fraction of young surviving from week 2 until week 7 showed a steady decline with season (Fig. 7b). The slope and the level of the decline was not significantly different between years (Table 3). We conclude that the annual and the seasonal variation in fledging success mainly arise from differences in mortality in the first 2 weeks of the parental care period.

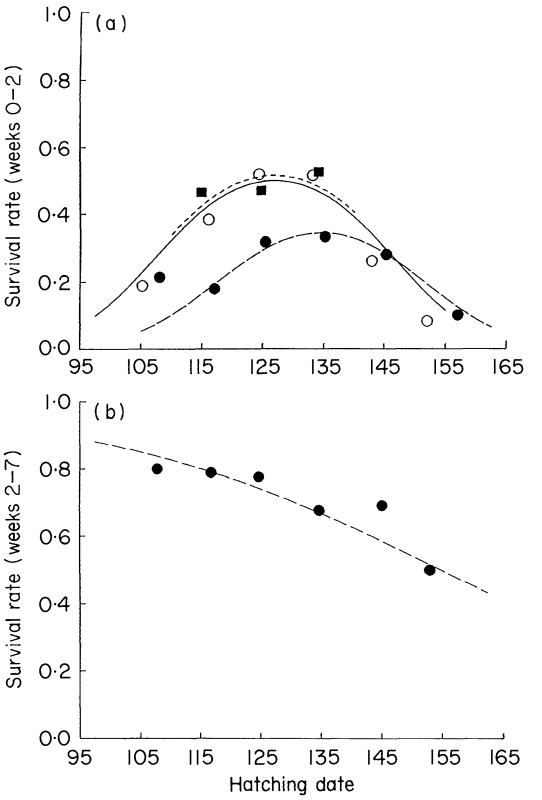

Fig. 7. (a) Seasonal variation in survival rate of young over the first 2 weeks after hatching (for control, advanced and delayed pairs combined) averaged over 10-day hatching periods, for 1988 (■), 1989 (○) and 1991 (●). (b) Seasonal variation in survival rate of young between week 2 and week 7 (for control, advanced and delayed pairs combined), averaged over 10-day hatching periods.

Discussion

TIMING DETERMINES FLEDGING SUCCESS

Fledgling production of foster parents with manipulated hatching dates was indistinguishable from fledgling production of control pairs whose eggs

Table 3. Logistic regression analysis of the survival of young over given periods after hatching. In the analysis data for control and experimental pairs were taken together. Significant parameters were determined over the periods between week 0 (hatching) and week 2 (model A), week 2 and week 7 (model B). For further explanation see Table 1

		(Increase in)			Estimates of coefficients		
Parameter		deviance	df	*P*	1988	1989	1991
A	Null model	334·2	171				
	Final model	255·7	165				
	Constant		1				
	Year	9·2	2	0·01	−41·16	−41·27	−47·03
	Actual date (*AD*)		1				
	Year × *AD*	7·3	2	0·03	0·65	0·65	0·69
	AD square	34·7	1	<0·01	−0·0026	−0·0026	−0·0026
B	Null model	218·4	148				
	Final model	208·4	147				
	Constant		1		5·42	5·42	5·42
	Actual date	10·0	1	<0·01	−0·035	−0·035	−0·035

hatched at the same time. We conclude, therefore, that fledging success is causally related to timing of breeding.

The manipulations did not exactly mimic what would happen in natural variations of timing. Birds of which the hatching date was advanced incubated their clutch for a shorter period and birds that were delayed had a prolonged incubation period, and this may have affected the outcome of the experiment. It is unlikely that the change in fledging success shown by experimental pairs was due to this bias. If the length of the incubation period affected fledging success, we would expect advancing the hatching date to result in an unidirectional change in fledging success throughout the season. This is clearly not the case, since advancing pairs in the first half of the season resulted in a reduced fledging success while the same manipulation resulted in an increased fledgling success in the second half of the season. The same argument applies to the effect of delaying the hatching date. We conclude, therefore, that the effect on incubation period does not explain our results. The absence of a noticeable effect of incubation period may be due to the fact that in coots both sexes take an equal part in the incubation load (Horsfall 1984c; Salathé & Boy 1987; for American coot: Ryan & Dinsmore 1979) which may leave each parent ample time to forage. Furthermore, it was shown for the American coot that body mass of both male and female did not change during the incubation period (Alisauskas & Ankney 1985), indicating coots are able to maintain energy balance during incubation.

Although as a result of our experiment the timing of parental care was manipulated, the hatching date of the eggs in the fostered clutch remained the same. A convex relationship between date and egg quality would therefore lead to the same results. In the coot, egg size is a good indication of egg quality as it reflects the quantity of yolk reserves available to the chick during embryonic development and predicts body mass at hatching (Horsfall 1984b). Egg size varies linearly, not quadratically, with date in all years (Fig. 3; J. Visser unpublished data). Furthermore, we found no association between egg size and fledging success. We conclude, therefore, that egg quality is not involved in the seasonal variation in fledging success.

COMPARISON WITH OTHER STUDIES

Parsons (1975), Hatchwell (1991) and Verhulst & Tinbergen (1991) used an experimental approach in which the timing of breeding was delayed by inducing repeat clutches through removal of the first clutch. The most important disadvantage of this method is that experimental birds incur the costs of laying an extra clutch, which could affect their quality. Furthermore, not all birds will lay a repeat clutch, which could lead to a biased sample of the population. Moreover, this method yields no date on the fitness consequences of an earlier timing of breeding. Parsons (1975) and Hatchwell (1991) studied colonial species, and both concluded that breeding success depended on timing relative to other individuals in the colony rather than on calendar date. Synchronization is of importance in colonial breeders to reduce vulnerability to predation. Synchronization is less important in territorial breeding species such as the coot or the great tit. In the great tit it was concluded that the seasonal decline in fledging success was due to differences in parental or territorial quality between early and late breeders, and not causally related to date (Verhulst & Tinbergen 1991).

MECHANISMS

What underlying mechanism could lead to the seasonal variation in fledging success in the coot? The analysis of weekly survival rates showed that the convex relationship between date and fledging success arises during the first two weeks after hatching (Fig. 7a). This period is critical for chick survival in most precocial species (e.g. Moss *et al.* 1981; Hill & Ellis 1984; Savard, Smith & Smith 1991). Coot chicks are totally dependent on their parents for food and for protection against predators and adverse weather conditions in the first 2 weeks (Horsfall 1984a). The young are fed predominantly with dipterans picked up from the water surface (Horsfall 1984a) and a convex seasonal pattern in diptera abundance is a possible explanation for the seasonal pattern in fledging success. Diptera abundance does, indeed, show a convex seasonal trend in Horsfall's study area (1984b), with maximum values in the first half of May, which coincides with the seasonal peak in fledging success in our study area. Experiments to test the hypothesis that seasonal variation in food availability is the factor responsible for the seasonal variation in fledging success are in progress.

The convex seasonal pattern could result from two separate seasonal relationships. If one process resulted in a seasonal increase in fledging success while another process resulted in a seasonal decline, the resulting relationship could be convex. The improvement in weather conditions could be responsible for an increase in fledging success. Cold weather early in the season might limit the available foraging time for the parents by increasing the brooding time (Erikstad & Andersen 1983; Beintema & Visser 1989). If there is a seasonal decline in reproductive value of fledglings, independent of fledgling quality, this leads to a seasonal decline in the optimal work rate (Daan *et al.* 1989). If this decline in reproductive value of fledgling coots exists, a seasonal decrease in parental effort may be the cause of the seasonal decrease in fledging success.

Whether a seasonal decline in parental effort exists remains to be investigated.

IS PARENTAL QUALITY NOT IMPORTANT?

The experiment clearly showed that differences in individual and/or territorial quality of the parents were not responsible for the seasonal variation in fledging success. This does not, however, imply that parental quality is not involved. Age is a potential measure of individual quality and in many bird species breeding success increases with age (review in Perdeck & Cavé 1992). We therefore tested whether age affected fledging success when the effect of date was taken into account. Controlling for date, the age of the male was positively correlated with fledging success (Fig. 8), whereas the female's age had no effect. Old males have larger and better territories (Cavé, Visser & Perdeck 1989) which may explain this relationship. We hypothesize, therefore, that variation in individual and/or territorial quality does play a role independent of the seasonal variation in fledging success.

ARE EARLY BIRDS TOO EARLY?

Birds laying early in the season would have achieved a higher fledgling production if they had postponed laying. Why don't they start laying later? To understand the individual bird's decision regarding laying date in an ultimate sense, fitness has to be quantified (Daan, Dijkstra & Tinbergen 1990). This concerns both the future survival and reproductive success of the fledglings as well as the residual reproductive value of the parents. There are reasons to assume that the values for both fitness-components decrease in the course of the season. Post-fledging survival declines with season in many bird species (e.g. Perrins 1970; Cavé 1968; Cooke, Findlay & Rockwell 1984; Dow & Fredga 1984; Newton & Marquis 1984; Hochachka 1990), and date has been shown to be causally involved in this relationship in the marsh tit (Nilsson 1990) and the great tit (Verhulst & Tinbergen 1991). The probability of starting a second clutch declines with date in coots (Perdeck & Cavé 1989). If this decline is directly related to date, the residual reproductive value of the parents might decline with date. These components together could result in a monotonic seasonal decline in total fitness, which would explain why some birds breed too early, as judged by the fledgling production of their first clutch alone. A better question may, therefore, be why the late birds do not lay earlier. Energetic limitations may play a role (Perrins 1970), since it has been shown in coots that supplementary feeding advanced laying date in 1 out of 2 years (Horsfall 1981). Furthermore, competition for nest sites or breeding territories may be important, forcing some individuals to breed later (Feldså 1973).

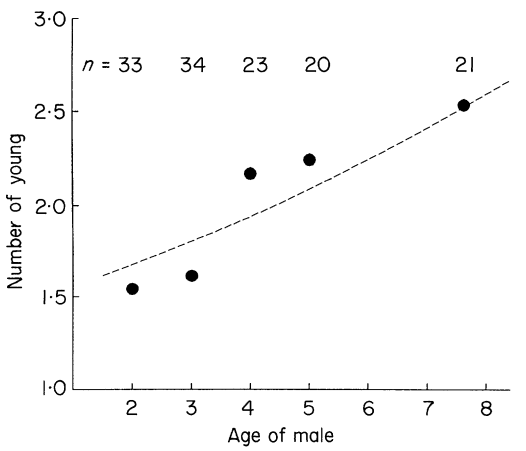

Fig. 8. Male age and fledging production. The effect of male age was independent of year, the actual date, the actual date squared and clutch size (variables present in Model C, Table 2).

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